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Size, Growth, and Reproduction of the Sandbar Shark, *Carcharhinus milberti*, in Hawaii[1]

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THE SANDBAR SHARK, *Carcharhinus milberti* (Müller & Henle 1841), is a wide-ranging species found in the subtropical and tropical areas of the Pacific, Atlantic, and Indian oceans. Investigations by Bigelow and Schroeder (1948), Springer (1960), and Clark and von Schmidt (1965) have resulted in a fairly thorough knowledge of the life history of the sandbar shark population in the western North Atlantic. Populations in other areas, however, differ in several respects. In a recent paper concerned with *C. milberti* in the East China Sea, Taniuchi (1971) documented differences in fecundity. The present study reveals significant differences in size at maturity, sex ratio, and fecundity for Hawaiian *C. milberti*.

The Cooperative Shark Research and Control Program (Tester, unpublished) afforded an excellent opportunity to gather life history data on inshore Hawaiian sharks. A total of 1,727 were captured of which 789 (45.7 percent) were sandbar sharks. The study species is pictured in Fig. 1 and can be distinguished from all other Hawaiian members of the Carcharhinidae by the relatively large first dorsal situated far forward (originating over the axil of the pectoral). It also has a prominent ridge between the two dorsals and dermal denticles that are widely spaced and nonoverlapping. It is a fairly heavy-bodied shark at maturity and can be various shades of gray or brown dorsally and creamy white ventrally. The tips and trailing edges of the fins of young individuals are usually white, but this coloration is generally lost by the time the shark has attained maturity. The teeth in the upper jaw are bladelike and broadly triangular. Those in the lower jaw are broad-based but the recurved cusps are thin and spikelike. The tooth formula for 15 Hawaiian individuals is:

$$\frac{14 \text{ or } 15\text{–}1 \text{ or } 2\text{–}14 \text{ or } 15}{12 \text{ to } 14\text{–}1\text{–}12 \text{ to } 14}$$

with

$$\frac{14\text{–}1\text{–}14}{14\text{–}1\text{–}14}$$

being the usual case.

METHODS

The Cooperative Shark Research and Control Program operated from July 1967 through June 1969 and was directed by Dr. Albert L. Tester (unpublished). Objectives of the program were to study the ecology of sharks present in inshore Hawaiian waters, to determine if shark abundance could be reduced by fishing effort, and to recommend future measures for controlling abundance.

The larger sharks were caught on a longline set overnight. Seventy-two hooks (size 14/0) were attached to the line at 20-fathom intervals. Hooks were generally baited with tuna although porpoise, eel, reef fish, cat, squid, or mackerel also occasionally were used. Over 200 sets were made parallel to shore at depths of 15 to 30 fathoms. Thirty-two sets were made at right angles to the depth contours with the shallow end anchored at about 10 fathoms and the deep end anchored at 60 to 100 fathoms. Smaller sharks were captured by handline or by a light longline (12 hooks, size 7/0) which was fished at 10 to 100 fathoms. Fishing methods will be detailed in a subsequent paper concerned with the distribution of Hawaiian *C milberti*.

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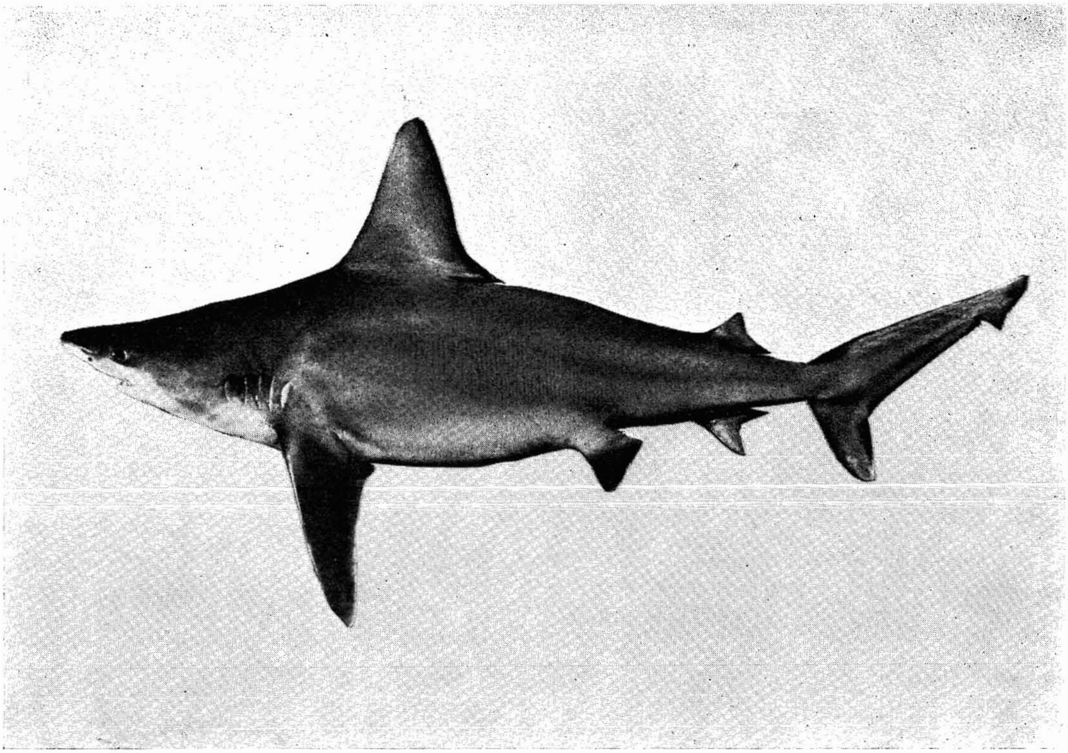

FIG. 1. A mature female *Carcharhinus milberti*. Precaudal length is 132.1 cm.

Live sandbar sharks (47 to 142 cm precaudal length) were maintained for periods of up to 30 months at the Kewalo Basin branch of the Hawaii Institute of Marine Biology. When the sharks had to be handled for measurement or observational purposes, they were first anesthetized with M.S. 222 (tricaine methanesulfonate). A variation of the method described by Gilbert and Wood (1957) was utilized. A 1:1,000 solution of the powdered anesthetic and seawater was prepared and placed in a 20-liter container. Sharks up to 90 cm precaudal length were netted out of the holding tank and immersed in the solution for 15 to 60 seconds. Larger sharks were anesthetized in the holding tank. The water level was lowered to a depth of 0.5 m and the shark was wrestled or lured over a net measuring 2.4 × 3.0 m which hung along the wall of the tank and extended out onto the floor. When the shark was in position, the net was lifted, thereby suspending the animal against the wall just above the waterline. M.S. 222 was then poured and squirted into the gill slits for 2 to 5 minutes until the shark ceased struggling. Only once did an individual show ill effects from the above procedure; a mature female failed to recover from what was probably an overdose of the anesthetic. No other problems were encountered during hundreds of anesthetizations.

RESULTS

Size

Total length (horizontal distance between the tip of the snout and the tip of the caudal in the normal swimming position) is dependent upon the angle at which the caudal is positioned and must be estimated if a portion of the caudal is missing. For *C. milberti*, which has a distinct precaudal pit on the dorsal surface of the caudal peduncle, precaudal length (horizontal distance between the tip of the snout and the deepest part of the precaudal pit) is a more consistent and accurate measure of size and will

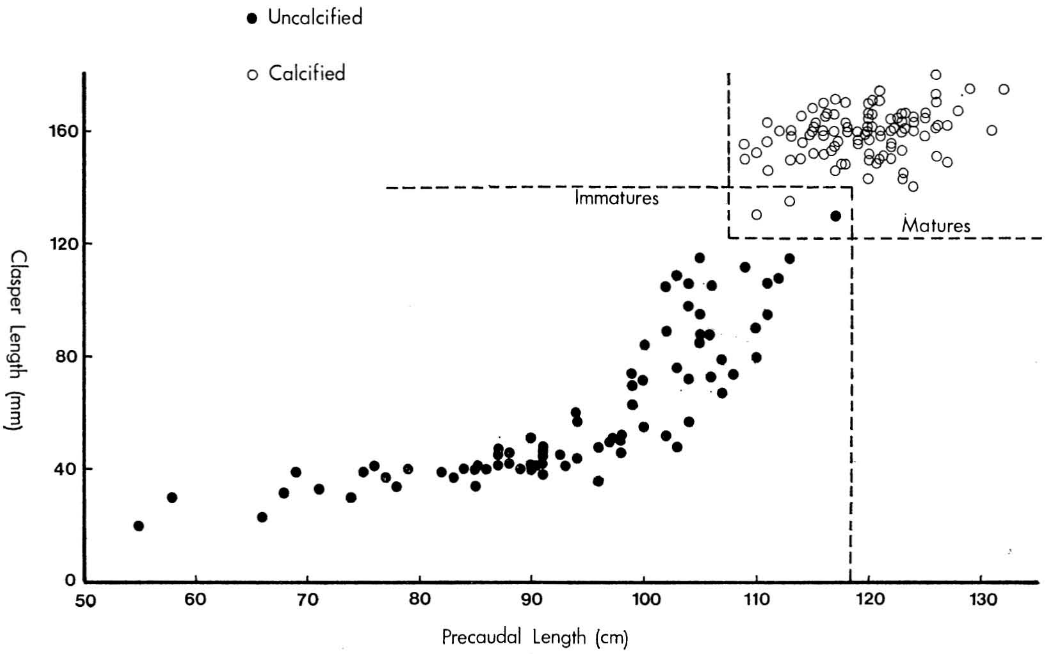

FIG. 2. Relationship between clasper length and precaudal length.

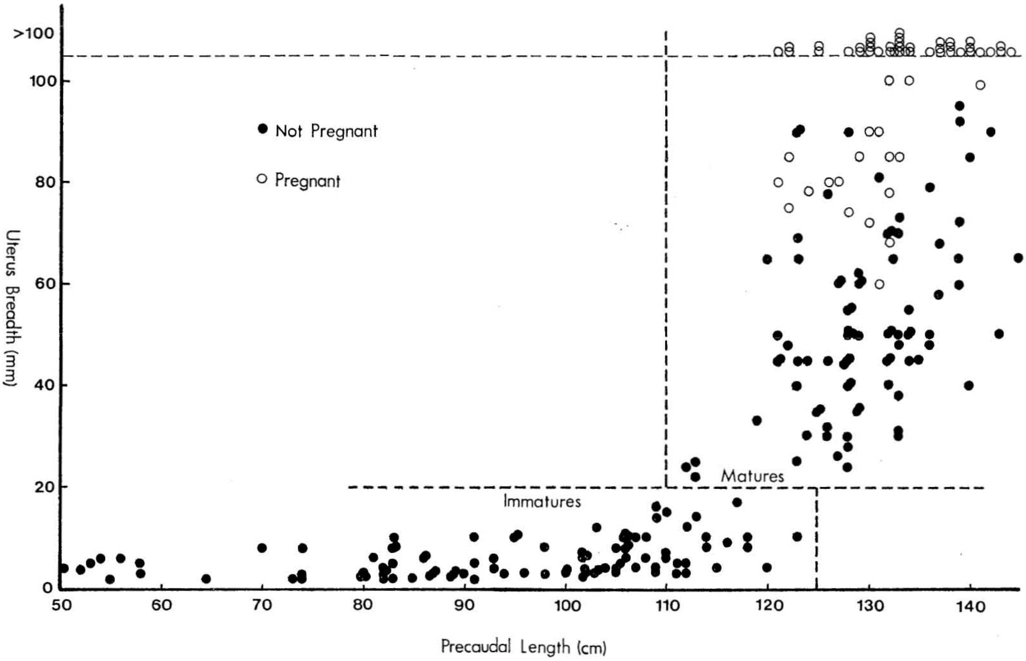

FIG. 3. Relationship between uterus breadth and precaudal length.

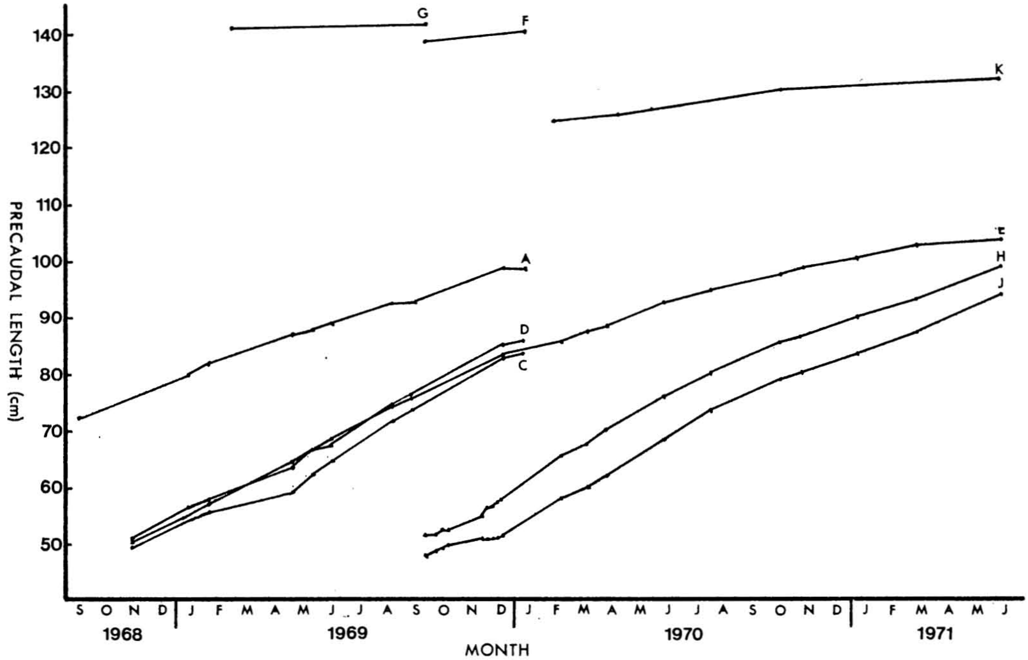

FIG. 4. Growth of captive sharks at the Kewalo Basin facility. Curves *A*, *E*, and *J* are males; curves *C*, *D*, *F*, *G*, *H*, and *K* are females.

generally be used in this report. The regression equation

$$\text{precaudal length} = 0.784\,(\text{total length}) - 3.022$$

can be used if only total length is known.

Shortly before male elasmobranchs attain sexual maturity, their claspers begin to lengthen rapidly. Enlargement of the testes to functional size is immediately followed by calcification of the clasper cartilages (Springer 1960). Minimum size at maturity for male *C. milberti* can be estimated by plotting clasper length (distance between the joint at the proximal end and the clasper tip) and calcification status against precaudal length (Fig. 2). It appears that males mature at an average length of about 110 cm with a minimum clasper length of 130 mm. Precaudal lengths of mature males averaged 119.4 cm and ranged from 109 to 132 cm. Calcified clasper lengths averaged 157 mm and ranged from 124 to 180 mm.

The breadth of the flattened uterus at the widest point can be used to determine sexual maturity among female sharks. A mature female is defined as an individual whose uterus breadth is at least as great as the breadth of a fully contracted uterus following parturition. Minimum size at maturity for female *C. milberti* was estimated by plotting uterus breadth against precaudal length (Fig. 3). It may be seen from the figure that the breadth of a fully contracted uterus is larger than 20 mm, so it appears that females reach maturity at a precaudal length of about 115 cm. Average size at maturity was 130.7 cm and the range was from 112 to 146 cm.

Of 90 juveniles captured, the smallest had precaudal lengths of 45, 48, 49, and 49 cm. Four pups born at the Kewalo facility measured 47.8, 51.0, 51.0, and 51.2 cm at birth. The largest embryos found within the uteri of pregnant females measured 50, 50, 49.5, and 49.5 cm. Precaudal length at birth, therefore, is generally between 45 and 51 cm. A value of 47 cm will be used below in calculations of growth rates.

Growth

Thirteen *C. milberti* lived for 4 months or longer in the large tank at Kewalo Basin. Eight

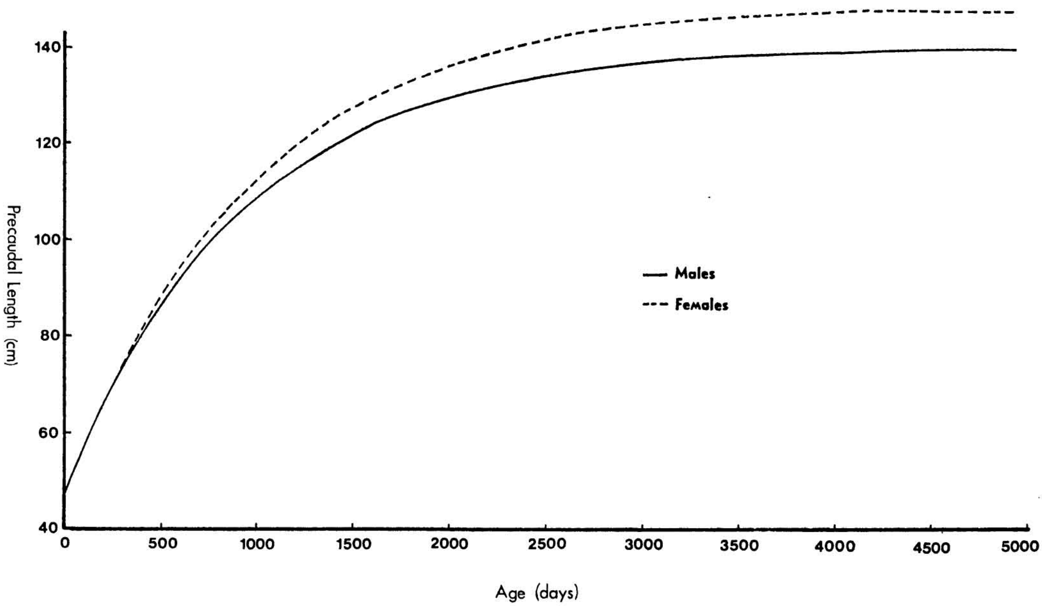

FIG. 5. Von Bertalanffy growth curves for captive sharks at the Kewalo Basin facility.
For males: $x = 139.4\,(1-0.6629\,e^{-0.001100t})$, where x is precaudal length (cm) and t is age (days).
For females: $x = 149.0\,(1-0.6845\,e^{-0.001026t})$.

of these died during the period of study, but all deaths occurred from unnatural causes (overdose of anesthetic, copper sulfate poisoning, or jumping out of the tank), and the animals appeared to be in good health at the time of their death. In fact, most lived longer than 8 months, the length of time listed by Clark (1963) as being the longest known period of captivity for the species.

The feeding program was determined arbitrarily since food requirements in the natural environment were unknown. The sharks were fed every 2 to 3 days but, instead of being fed a set amount each period, they were simply thrown morsels of food until their rate of feeding decreased markedly. They were usually fed cut pieces of frozen skipjack (*Katsuwonus pelamis*) or akule (*Trachurops crumenopthalmus*), but frequently they also were fed fresh or frozen red snapper, jack, eel, small reef fish, smelt, octopus, and squid. The sharks seemed to prefer frozen smelt, a fish which does not occur in Hawaii, above all else.

At 1- to 8-week intervals the sharks were anesthetized and their precaudal lengths measured. The growth data obtained are plotted for nine of the animals in Fig. 4. The four growth curves which do not appear in the figure are almost identical to curves *C* and *D* but have not been plotted because of space limitations.

Von Bertalanffy curves were fitted to the data using the method of Fabens (1965). The equation for males, based on 49 growth increments of four sharks is:

$$x = 139.4\,(1-0.6629e^{-0.001100t}),$$

where x is precaudal length (cm) and t is time since birth (days). The curve is plotted in Fig. 5. The calculated value for asymptotic size is 139.4 cm, this value being a little larger than the length of the largest male captured in the field (132 cm). Comparison of the theoretical average length at the end of 1 year (77 cm) with the interpolated lengths for actual data at the end of 1 year (assuming each individual was born at a length of 47 cm) for curves *E* (78 cm) and *J* (77 cm) in Fig. 4 indicates a remarkably close fit. It appears, therefore, that the von Bertalanffy equation adequately describes the growth of captive males at the Kewalo Basin facility.

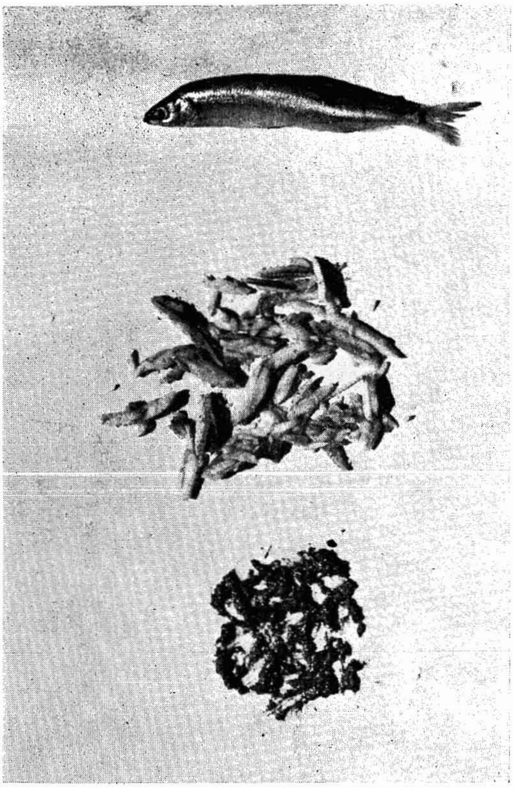

FIG. 6. Smelt from stomachs of *Carcharhinus milberti*. Top, fresh; middle, after 24 hours' digestion; bottom, after 48 hours' digestion.

Growth data from captive females also fit the model well. The equation, based on 57 growth increments of nine sharks, is:

$$x = 149.0\,(1-0.6845e^{-0.001026t}).$$

This curve also is plotted in Fig. 5. Again, the theoretical asymptotic size (149.0 cm) is slightly larger than the largest individual captured in the field (146 cm). Theoretical length after 1 year's growth is 78 cm, a figure which closely approximates the interpolated lengths for actual data after 1 year's growth for curves *C* (77 cm), *D* (79 cm), and *H* (80 cm) in Fig. 4.

Field data indicate that mature females are larger than mature males. Likewise, the theoretical asymptotic size derived from the von Bertalanffy equation is larger for females than for males. Fig. 5 indicates that males reach their minimum mature size (110 cm) at 1,050 days (about 3 years) and that females attain mature size (115 cm) in a similar length of time (1,070 days).

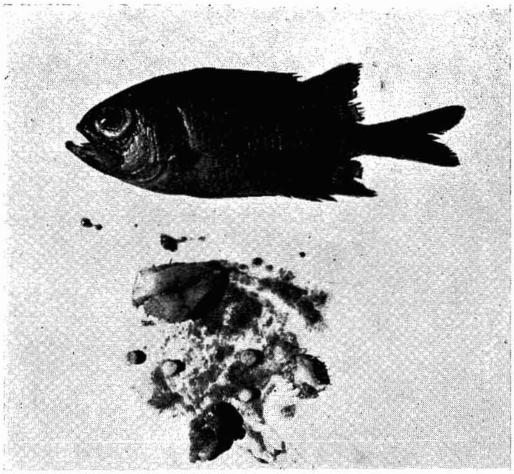

FIG. 7. Squirrelfish from stomach of *Carcharhinus milberti*. Top, fresh; bottom, after 48 hours' digestion.

If the rate of digestion is known, then the feeding frequency of sharks in the field can be roughly estimated from the percentage of stomachs containing food. To this end, three captive *C. milberti* of approximately the same size (95 to 101 cm precaudal length) were starved for 4 days and then were fed smelt or squirrelfish until they were satiated. The smelt—narrow-bodied fish with thin skin and soft flesh—were about 15 cm long. The squirrelfish were of similar length; but these fish are much deeper-bodied and have large and heavy scales and firm flesh.

Two *C. milberti* which had been fed smelt were killed 24 and 48 hours after being fed and their stomach contents were examined (Fig. 6). At 24 hours small chunks of flesh and bones were recognizable amidst a gray mush of oil droplets and flocculated particles. At 48 hours the mush was darker in color and more condensed. A few oil droplets were still visible but all flesh and bones had been broken down.

Only one shark was fed squirrelfish. When its stomach contents were examined 48 hours later (Fig. 7), flesh, bones, and eye lenses were still present in the light-colored mush of oil droplets and flocculated material.

The death of several captive sharks as a result of copper sulfate poisoning yielded further data on digestive rates. The animals had been fed whole (25 cm long) and cut akule about 30 hours earlier. When their stomach contents were examined, it was found that some of the akule were still whole and most of the flesh remained on the bones, the implication being that digestion had only just begun.

Apparently, food is retained within the stomachs of *C. milberti* for about 2 days if the prey is small and soft. Three to 4 days are required for average-sized prey to pass through the stomach, and more than 4 days are probably required for large and hard-to-digest items. Captive sharks at Kewalo probably always had food in their stomachs because they were fed every 2 or 3 days.

Only 45 percent of the *C. milberti* captured during the Cooperative Shark Research and Control Program had food in their stomachs. It may be argued that sharks with empty stomachs would be more likely to take a baited hook, so this value may be biased and, therefore, too low. However, the data do indicate that large numbers of sandbar sharks had empty stomachs. When food was present, the amount was often much less than stomach capacity. It appears, therefore, that captive sharks at Kewalo were fed more than they would normally have acquired in their natural environment and at shorter intervals. Consequently, the growth rates determined above are probably greater than normal, and Hawaiian sandbar sharks probably require more than 3 years to reach maturity in the field.

Moss (1967) used a rather indirect method to determine growth rates for lemon sharks (*Negaprion brevirostris*). Rate of tooth replacement and size difference between functional and replacement teeth are the basic data required. Age at maturity can be calculated if one knows the lengths at birth and maturity, the number of tooth generations between birth and maturity, and the mean length of time each generation is functional.

Functional teeth along the outer border of the jaw are constantly being lost and replaced by younger teeth through a process which has been summarized by Moss (1967). Rate of replacement appears to be relatively constant on a short-term basis and is independent of wear or injury to individual teeth. Ifft and Zinn (1948) found that the teeth of the smooth dogfish (*Mustelis canis*) are replaced at the rate of one row every 10 to 12 days. Märkel and Laubier (1969) concluded that a tooth generation is replaced every 5 weeks in the cat shark (*Scyliorhinus canicula*). The most comprehensive study of tooth replacement is that by Moss (1967) on young lemon sharks (49.5 to 80.2 cm in body length). After studying a group of healthy animals that were regularly fed, he calculated a mean functional tooth life of 7.8 days for teeth in the upper jaw and 8.2 days for teeth in the lower jaw. The present investigation was patterned after this study.

Captive sharks were anesthetized and the cusps of alternate functional teeth of the first eight series on either side of the symphysis of the upper jaw were clipped with wire cutters. Care was taken not to damage nerves and blood vessels in the pulp cavity or in the surrounding gum tissue. The procedure resulted in eight recognizable teeth without seriously impairing the shark's ability to use its teeth for grasping and slicing food. At subsequent 4- to 10-day intervals, marked teeth still in position were counted.

The imbricated and overlapping pattern of tooth position in the jaws of *Carcharhinus milberti* requires that the teeth be lost individually. Consequently, the measure of replacement rate is termed mean functional tooth life and is defined as the mean number of days a tooth remains in the functional position. Among the carcharhinids, only a single tooth of each series in the upper jaw is functional.

The mean functional tooth life for each shark was determined from regression of the number of marked teeth remaining in position plotted against the number of days elapsed since the teeth were marked, with the number of teeth originally marked being the origin. The X intercept (number of days when zero marks are present) is the estimate of mean functional tooth life. The relationship between tooth life and precaudal length is plotted in Fig. 8. Though the data are highly variable, it is plain that tooth life increases with size. Previous investigations have not shown this because they involved only juveniles or individuals of the same size. Mean tooth life ranged from 18 days for very young individuals (50 cm precaudal

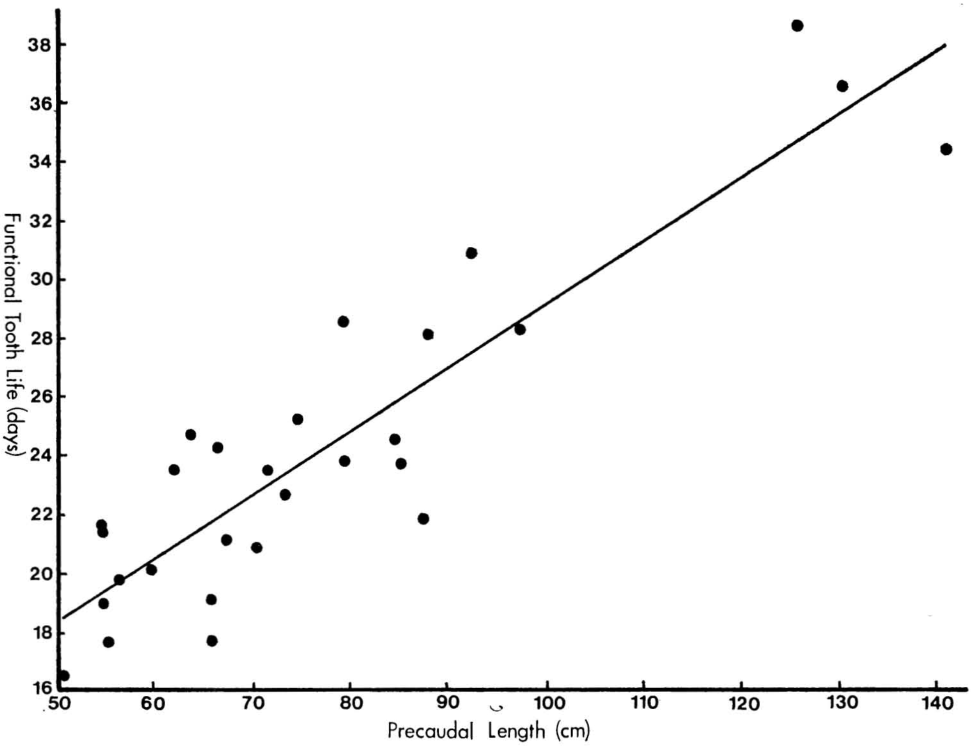

FIG. 8. Relationship between mean functional tooth life and precaudal length. $Y = 0.215X + 7.63$, where Y is functional tooth life and X is precaudal length.

length) to 36 days for mature sharks (130 cm precaudal length).

The procedure for determining the number of tooth generations between birth and maturity has been described by Moss (1967) as follows:

> Strasburg (1963) demonstrated that tooth growth in elasmobranchs could be considered as occurring in increments of instantaneous growth, each increment occurring at the time of replacement. Thus, tooth width plotted against body length provides a stepped type of curve for any growing shark. By reason of the fact that the teeth in the first replacement row are larger than the older, functional ones, the effective growth increments of the teeth at the time of replacement can be measured. By plotting regressions of functional tooth width and replacement tooth width against body length, a set of nearly parallel lines is produced. These are then connected by horizontal and vertical tie lines.

The number of vertical tie lines between size at birth and size at maturity represents the number of tooth generations preceding maturity.

The age at maturity was calculated by solving the regression in Fig. 8 for every precaudal length corresponding to a vertical tie line obtained from the foregoing method. This yielded a tooth life for each generation. These were summed to get age at maturity, the calculations yielding estimates of 10.2 years for males and 13.1 years for females. Data variability and questionable assumptions reduce the estimates to only rough approximations. One assumption, which is almost certainly violated, is that tooth replacement rate is the same for captive sharks at Kewalo as it is for animals in the field. Replacement rate is inversely correlated with growth rate, and growth at Kewalo was probably more rapid than in the field. It was assumed that there is no difference in rate of tooth replacement for males and females of equal size, but, if their growth rates do differ, replacement rates may also differ. A final assumption is that the relationship between functional tooth life and body length is linear. It

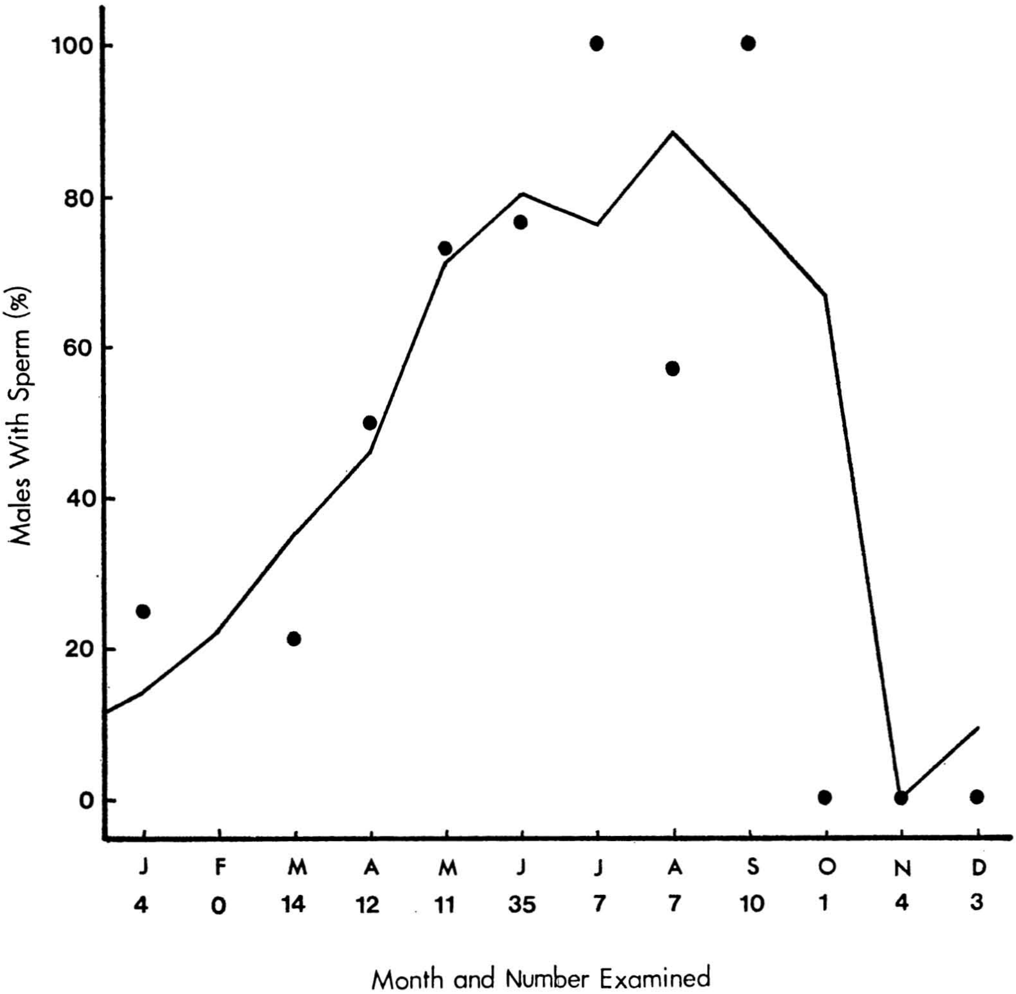

FIG. 9. Monthly percentages of mature males with sperm in seminal vesicles. The line is a running average of the three nearest values.

may actually be curvilinear if there is a direct relationship between growth rate and tooth life.

The two methods used to estimate age at maturity yield widely disparate results. The real value probably lies somewhere in between but will likely never be known unless a successful tag-and-recapture study is conducted. Eighty-six *C. milberti* were tagged and released around Oahu and Niihau during the present investigation, but only one was recaptured. It was a mature male which showed no growth during its 595-day period of liberty.

Reproduction

The sex ratio of embryos does not deviate significantly from 1:1. Of 308 embryos from 55 litters of Hawaiian *C. milberti*, 152 (49.4 percent) were males. Apparently, the sex ratio for mature individuals is also 1:1. Forty-five adult females and 47 adult males were captured on 32 longline sets which were made at right angles to the depth contours and which extended from a depth of about 10 fathoms out to a depth of about 80 fathoms. This fishing procedure exerted approximately equal effort over almost the entire depth range of the species.

The mating season for carcharhinids can be ascertained in several ways. Among the males, vascular congestion about the cloacal area at the base of the claspers and the presence of sperm in the seminal vesicles indicate the arrival of the mating season. Mature ovarian eggs and fresh mating wounds are indicative of the mating season for females. Eggs in the uteri which have not yet begun development are further evidence.

If the percentage of mature male *C. milberti* with sperm in their seminal vesicles is plotted against the month of observation (Fig. 9), the data tend to peak during the summer. The highest percentages were found in July and September. Vascular congestion about the claspers was also noted during the summer months. Data from mature females also indicate a summer mating season. The average diameter of the four largest ovarian eggs was generally small (10 to 15 mm) during the fall but began to increase during the spring when the eggs assume a reddish yellow coloration. Eggs attained the size at which ovulation occurs (35 to 40 mm) during June, July, and August. In addition, 11 females were captured between 23 July and 18 August that had recently ovulated eggs in their uteri. Fresh mating wounds were also observed on several of these individuals.

Springer (1960) discussed the development of *C. milberti*; and TeWinkel (1950), Amoroso (1960), and Schlernitzauer and Gilbert (1966) have provided comprehensive discussions of the embryology of live-bearing sharks. The embryology of *C. milberti* in Hawaii is similar to that of other carcharhinids and will be briefly summarized.

Only the right ovary is functional. Approximately 8 months before ovulation, several ova begin enlarging and turn reddish yellow as yolk is deposited. Upon reaching a diameter of 35 to 40 mm, about five or six ova are released from the ovary and proceed through the body cavity, ostium, and right or left shell gland to the uteri. Prior to maturity the uteri are less than 20 mm in breadth but, at maturity, they enlarge and reach breadths of about 60 mm at ovulation. They continue to expand and thicken as the embryos grow. Following parturition they contract to a breadth of 20 to 40 mm. Initially the embryos derive their nourishment solely from the stored yolk. Later, they may also absorb nutrients from fluids in the oviducts. When the embryo reaches a length of about 30 cm, a pseudoplacenta is formed from the yolk sac which allows the exchange of gases, nutrients, and waste products between the embryo and the mother for the remainder of the gestation period (Springer 1960).

Both uteri are equally functional. Of 499 embryos collected from 90 pregnant females, 245 (49.1 percent) were in the right uterus.

Average embryo size is plotted against date of measurement in Fig. 10 for 80 *C. milberti* litters. The points intersect with the zero ordinate during the months of July, August, and September, indicating that this is when development began. These data agree with the time-of-mating estimates already discussed. Total lengths at birth averaged 64 cm (47 cm precaudal length). Because embryos attained this size and were born during July, August, and September, they must have had a gestation period of about 12 months. Further credence is lent to the theory of a summer pupping season by the fact that the smallest free-swimming individuals were caught during the late summer and early fall. Corroborative evidence was also furnished by the two sandbar sharks which gave birth after being hauled aboard the fishing vessel during the middle of September and by the numerous spent females with enlarged, flabby uteri captured during the months of September and October.

Forty-two percent of the mature female *C. milberti* captured in Hawaii were pregnant. The average number of embryos in 91 litters examined was 5.5 (range: 1 to 8). Females holding full-term embryos and those that had recently given birth did not possess ripe ova. If a 1-year gestation period is assumed, a minimum of 2 years would then be required for the reproductive cycle. A 2-year cycle is probably the rule because, as mentioned, about half (42 percent) of the mature females were pregnant. Completely healed mating scars underlying fresh bite wounds found on some recently impregnated females were evidence that more than a single litter may be produced. The

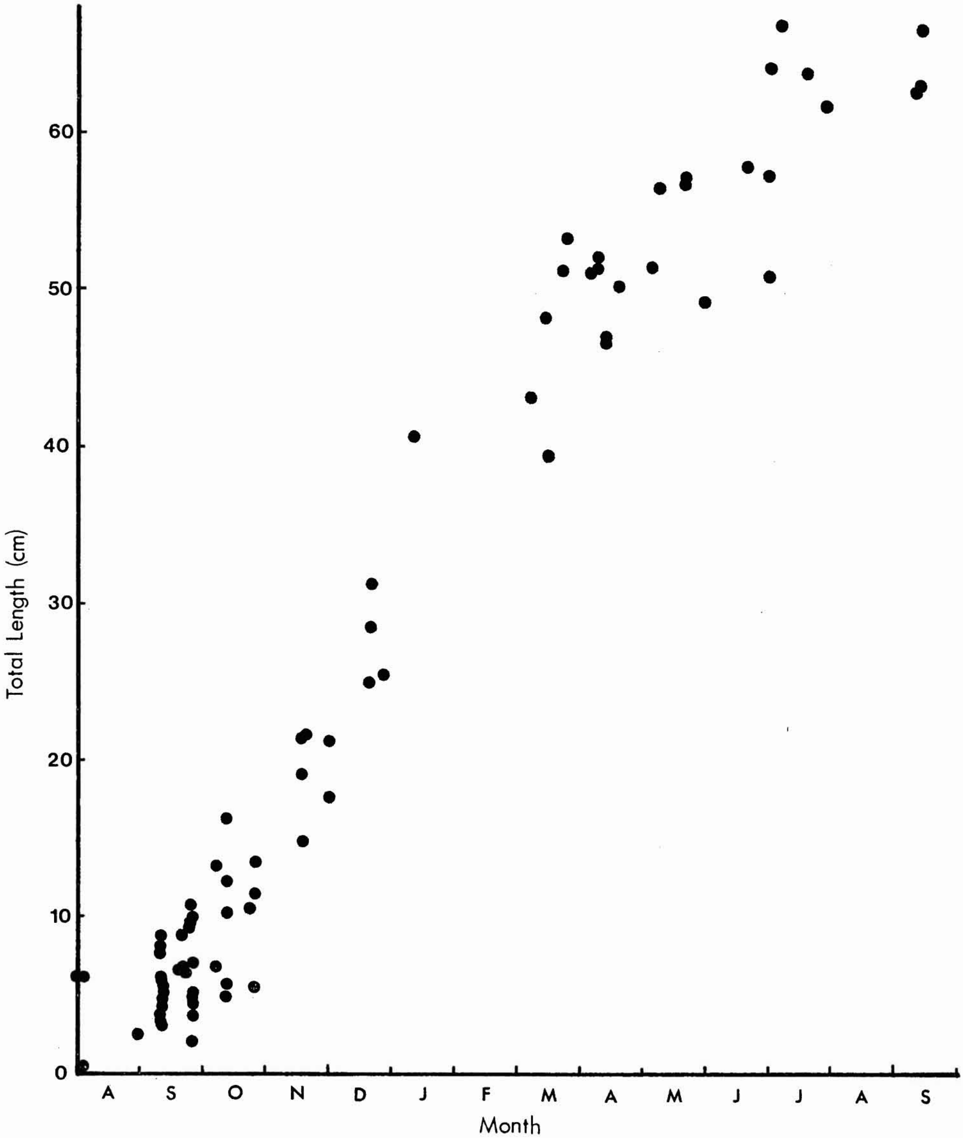

FIG. 10. Monthly average total lengths of embryos in letters of Hawaiian *Carcharhinus milberti*.

total number of litters borne by the average female, however, cannot be estimated because the life-span is unknown.

A sandbar shark captured on 27 December 1968 and held at the Kewalo facility gave birth to four viable pups on 24 September 1969. Because I observed the births and because I have found no account of the actual process in the literature, I will describe the event here. At 1600 hours, I guided "Sandy" into a net hanging along the wall of the main tank. She struggled for 3 to 4 minutes before succumbing to the anesthetic and was then laid on a low table in the tank while length measurements (138.6 cm precaudal length) and tooth replacement data were taken. Sandy was rather heavy-bodied when captured 9 months earlier and her girth had increased considerably since she was placed in the tank. On this day I noticed vascular congestion and edema about the cloacal region for the first time. When I stuck my finger through the cloacal aperture, I felt the tail of an embryo. I must have ruptured the shell membrane at this time because fluid spilled from the opening when I withdrew my finger. When the observations were completed, the anesthetic was flushed from Sandy's system by "walking" her around the tank for about 5 minutes until she began swimming on her own. About 10 minutes later, the tail of an embryo was protruding from her cloaca. I pulled the embryo out, and placed it in a smaller observation tank where it soon began swimming normally.

By 1800 Sandy had recovered from the anesthetic but was swimming more rapidly than was her usual habit. The tails of two more embryos were protruding about 15 cm from her cloaca, swinging back and forth in unison with the caudal fin and peduncle area of the mother. At 1845 I saw a newborn pup swimming awkwardly around the tank and, because the posterior half of the third embryo was visible, another birth appeared imminent. I reentered the tank, which was now about 1 m deep, to observe the birth. Sandy was swimming at twice her normal rate and making frequent sharp turns. When more than half of the embryo was protruding, she made a quick 180° turn and left the pup at her pivot point. It sank slowly to the bottom making feeble, but uncoordinated, swimming movements. It lay on its side for 15 to 20 seconds, opening and closing its mouth and presumably pumping water over its gills. Then it wriggled rapidly but awkwardly to the surface for 4 or 5 seconds before sinking slowly to the bottom again. Bursts of swimming toward the surface followed by decreasing periods of rest on the bottom were repeated several times. Gradually, the rate of swimming slowed and became more coordinated. Fifteen to 20 minutes after its birth the pup was swimming continuously with a coordinated but slightly more rapid motion than is normal for older individuals and in a more sinuous fashion—probably because the vertebral and caudal cartilages had not yet calcified.

A fourth embryo was born live and four others were stillborn. By 1945 Sandy had slowed to her normal swimming rate and had ceased her frequent turning maneuvers. The umbilical cords were still trailing from her cloaca. On the following day they were found on the bottom of the tank along with the remains of the pseudoplacentas and egg cases.

The pups were measured the day following their birth. The lengths of the live pups were: female, 67 cm total length, 51.2 cm precaudal length; female, 67 cm total length, 51.0 cm precaudal length; male, 67 cm total length, 51.0 cm precaudal length; and male, 63 cm total length, 47.8 cm precaudal length. The pups were all larger than 47 cm precaudal length which is the estimate of average length at birth derived from field data. This is probably because they were also born later in the season than is usual for *C. milberti*. The conditions of confinement may have prolonged their period of prenatal development.

Total lengths of the stillborns were: male, 33 cm; male, 33 cm; female, 32 cm; and female, 32 cm. It is believed that stillborns are rare among Hawaiian *C. milberti* inasmuch as dead embryos were seldom found in the uteri of captured specimens. Those occurring in the tank were probably the result of an injury sustained by the mother during capture or confinement.

Neither the pups nor their mother showed interest when food was offered about 4 hours after birth. On the following evening, however, Sandy fed well. Four days after birth at least one pup was observed feeding, and all took food on the 5th day.

At parturition a 1-cm remnant of the umbilicus protruded through a slit in the belly of each pup. This was absorbed after 2 weeks and the slit closed a week later, leaving an obvious scar. During this 3-week period, the average increase in precaudal length of three pups (one was sacrificed at birth) was 1.2 cm. Umbilical scars had completely disappeared at 6 months of age, during which time the average increase in precaudal length was 15.8 cm.

DISCUSSION AND SUMMARY

Mature Hawaiian *C. milberti* are smaller than their conspecies in other areas. Hawaiian males mature at precaudal lengths of about 110 cm, the largest male measuring 132 cm. Females mature at about 115 cm and the largest measured 146 cm. Springer (1960) found that minimum lengths at maturity in the western North Atlantic correspond to precaudal lengths of 138 cm for males and 140 cm for females and that the largest measured 174 and 180 cm, respectively. Wheeler (1962) found that males in the Mauritius-Seychelles area mature at a total length of 170 cm, a length which corresponds to a precaudal length of 130 cm; and that females as large as 128 cm precaudal length were still immature. J. Bass (personal communication) reported that male *C. milberti* from South Africa mature at a precaudal length of 115 cm and attain a maximum precaudal length of 140 to 145 cm.

Size differences may result from different water temperatures. Hawaiian surface temperatures measured during the Cooperative Shark Research and Control Program were uniformly high. Quarterly averages were: spring, 25.2° C; summer, 26.9° C; fall, 26.9° C; and winter, 24.3° C. Surface temperatures in the western North Atlantic and off the coast of South Africa are generally cooler and more variable. In addition, sandbar sharks in these areas migrate to cooler waters during the summer months.

Size at birth is about the same in both the Pacific and Atlantic oceans. Springer (1960) reported a total length corresponding to a precaudal length of 45 cm for Atlantic sharks. Precaudal lengths for Hawaiian individuals averaged 47 cm. Taniuchi's (1971) estimate for *C. milberti* in the East China Sea corresponds to precaudal lengths between 48 and 56 cm.

C. milberti held captive at Kewalo Basin for periods of 4 to 30 months showed growth rates indicating a birth-to-maturity span of about 3 years. They showed an average growth of about 31 cm the 1st year, 21 cm the 2nd year, and 16 cm the 3rd year. Females grew slightly faster than did males.

The procedure based on rate and number of tooth replacements yielded age-at-maturity estimates of about 10 years for males and 13 years for females. Both the 3-year and the 10- to 13-year estimates are subject to large sources of error. The true value probably lies somewhere in between. Springer (1960) believes that growth from birth to maturity takes about 2 years in the Atlantic, though he admits this estimate is based on little real evidence.

Tooth replacement rates calculated for Hawaiian *C. milberti* indicate a mean functional tooth life of 18 days for young sharks to 36 days for mature individuals. Replacement rates have not been calculated for sandbar sharks in other areas, but the above figures are within the range of values determined for other species.

At birth the sex ratio of Hawaiian *C. milberti* is 1:1. Springer (1960) found the same ratio (50.0 percent males) for 65 litters as did Clark and von Schmidt (1965) for 21 litters (47 percent males) and Taniuchi (1971) for 91 litters (46.6 percent males). The sex ratio for mature Hawaiian sandbar sharks caught on right-angle sets during this study is also 1:1. Springer (1960), however, found a sex ratio of about five females to one male in the western North Atlantic. Likewise, Clark and von Schmidt (1965) concluded that the sex ratio for *C. milberti* in the central Gulf Coast region of Florida was 6:1. Springer feels that courtship behavior may be responsible for the uneven sex ratio. He believes that males do not feed during this period but females are not so inhibited and may fatally injure the males. Apparently, this is not the case in Hawaii.

Data from several sources indicate that the mating season for Hawaiian *C. milberti* peaks during July and August. Springer (1960) found an earlier mating season in the waters off southeastern Florida and concluded that June is the period of maximum mating activity. Taniuchi (1971) believes that sandbar sharks in the East China Sea mate during June and July. Hawaiian *C. milberti* are also born during the summer, so their gestation period would be about 12 months. Springer (1960) estimated a gestation period of 9 months with limits of 8 to 12 months. Taniuchi (1971) reported a gestation period of 10 to 12 months.

Hawaiian litters averaged 5.5 embryos compared to an average of nine embryos per litter in Florida (Springer 1960, Clark and von Schmidt 1965). Wheeler (1962) found an average of 8.3 embryos and Taniuchi (1971) found an average of 6.0 embryos. When the relationship between litter size and length of the mother was examined for all pregnant *C. milberti* caught in Hawaii, a highly significant, positive regression was found. Hawaiian sandbar sharks probably have smaller litters than their conspecies in other areas because the females are smaller when they give birth.

In Hawaii 42 percent of the mature females were pregnant. This is considerably higher than the values of 17 percent, 18 percent, and "substantially less than 1/3" calculated by Springer (1960) for *C. milberti* off the east coast of Florida and the value of 27 percent determined by Clark and von Schmidt (1965) for the central Gulf Coast of Florida. Springer attributes the low percentages in Florida to a scarcity of males. Seven of the 15 mature females Wheeler (1962) caught in the Mauritius-Seychelles area were pregnant.

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